Elevated atmospheric humidity shapes the carbon cycle of a silver birch forest ecosystem: A FAHM study

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HIGHLIGHTS

- Climate change may affect carbon (C) balance of forests.
- C input and output fluxes were estimated for humidified and control forest ecosystems.
- Humidified birch stands were C sinks, but control stands can be considered as C neutral.
- Elevated air humidity increased remarkably the C input to the soil.
- Humidification increased C sequestration in understory but decreased it in trees.

GRAPHICAL ABSTRACT
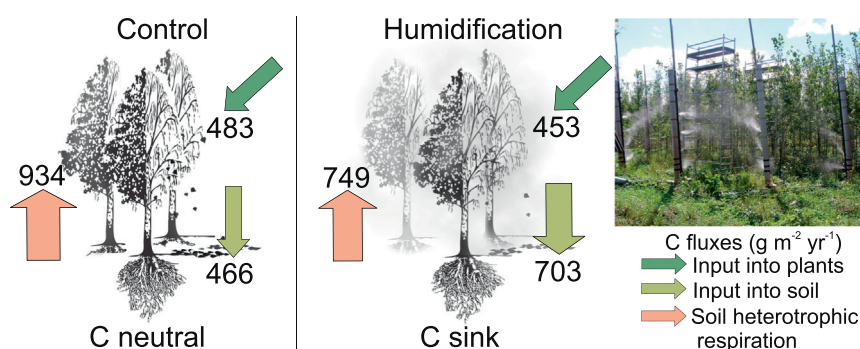
ABSTRACT

Processes determining the carbon (C) balance of a forest ecosystem are influenced by a number of climatic and environmental factors. In Northern Europe, a rise in atmospheric humidity and precipitation is predicted. The study aims to ascertain the effect of elevated atmospheric humidity on the components of the C budget and on the C-sequestration capacity of a young birch forest. Biomass production, soil respiration, and other C fluxes were measured in young silver birch (*Betula pendula* Roth) stands growing on the Free Air Humidity Manipulation (FAHM) experimental site, located in South-East Estonia. The C input fluxes: C sequestration in trees and understory, litter input into soil, and methane oxidation, as well as C output fluxes: soil heterotrophic respiration and C leaching were estimated.

Humidified birch stands stored C from the atmosphere, but control stands can be considered as C neutral. Two years of elevated air humidity increased C sequestration in the understory but decreased it in trees. Humidification treatment increased remarkably the C input to the soil. The main reason for such an increase was the higher root litter input into the soil, brought about by the more than two-fold increase of belowground biomass production of the understory in the humidification treatment. Elevated atmospheric humidity increased C sequestration in young silver birch stands, mitigating increasing CO_2 concentration in the atmosphere. However, the effect of elevated atmospheric humidity is expected to decrease over time, as plants and soil organisms acclimate, and new communities emerge.

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1. Introduction

The study of the responses of forest ecosystems to climate change, especially contributing to the basic understanding of the link between carbon (C) and nutrient cycling, belongs to frontline science (Graven et al., 2013; Kasurinen et al., 2016; Keenan et al., 2013; Oren et al., 2008; Schaphoff et al., 2016). Global temperature increase enhances evaporation, and warmer air can hold more water vapour. However, global climate change is expressed differently in different regions - scenarios on future climate changes in Europe predict a rise in atmospheric humidity and precipitation in Northern Europe and a reduction in the south (IPCC, 2007, 2013); annual precipitation has increased already since 1900 and near-surface specific atmospheric humidity since 1970 (IPCC, 2013).

Owing to the accelerating rise in atmospheric CO_2 globally, C sequestration in ecosystems is a very actual topic. Global scale studies have revealed that forest ecosystems in the Northern hemisphere are functioning as significant sinks for atmospheric CO_2 (Goodale et al., 2002). However, it is not clear how forest C cycling and C sequestration are affected by increased humidity. Processes determining the C balance are influenced by a number of climatic and environmental variables; hence the changing climate probably brings about shifts in C dynamics and balance (Malhi et al., 2015). The greater sequestration of C in forest biomass and soil as a result of climate warming and increasing CO_2 concentration is one of the most desired solutions mitigating global environmental risks, but the sequestration is at the same time limited by the availability of mineral nutrients, particularly nitrogen in the soil (Millard et al., 2007). However, Eggers et al. (2008) predict that the role of forests as C sinks may change towards the end of the century, when increasing drought and disturbance risks could turn forests into a source of C.

Whether the forest ecosystem is a C sink or source is determined by the balance between C gain and C loss. C taken up by photosynthesis can be accumulated both in plant biomass and in the soil (by litter input mainly). C loss occurs mainly as a result of autotrophic and heterotrophic respiration, leaching, and photo-oxidation. C budget is shaped by soil processes and plant physiological functioning, resulting in changes in soil properties and plant biomass accumulation. The C balance will change if forest cutting, fire, or other disturbances release great amounts of previously stored C to the atmosphere within a short time period after the disturbance. Generally, young stands (<10 years) are C sources in the temperate zone (Pregitzer and Euskirchen, 2004). The time until a secondary succession forest changes from a C source to a C sink is very site-dependent; hence every additional study contributes to more accurate generalizations and models.

Forest ecosystems contain up to 80% of all aboveground terrestrial C and 40% of all belowground terrestrial C (Dixon et al., 1994); therefore even small shifts in the balance between photosynthesis and ecosystem respiration can result in a large change in the uptake or emission of CO_2 between forests and the atmosphere. Hence the studies about the effect of climate change components (shifts in regional rainfall and humidity, increases in temperature, increasing atmospheric CO_2 etc.) on forest C dynamics are especially important for predicting the C balance in the future.

Previous studies in the FAHM experiment have shown that elevated air humidity causes lower transpiration, leading to an increase in soil moisture (Kupper et al., 2011). Although microbial biomass remained unchanged, total soil respiration (CO_2 emission) decreased (Kukumägi et al., 2014). Also fluxes of other greenhouse gases changed: CH_4 consumption was lower and N_2O emission decreased (Hansen et al., 2013). Humidification decreased above- and belowground biomass of trees (Sellin et al., 2015) but doubled understory belowground biomass and production (Kukumägi et al., 2014). Lower transpiration (Kupper et al., 2011) and photosynthesis of birch leaves led to a decrease in aboveground growth (Sellin et al., 2013); longer lifespan of leaves (Godbold et al., 2014), higher specific area of leaves (Sellin et al., 2013; Rosenvald et al., 2014) and of ectomycorrhizal (EcM) roots

(Parts et al., 2013) are among the acclimation tools for recovering tree functional activity in elevated humidity stress conditions. However, the published results were not sufficient for compiling the carbon budgets of silver birch stands growing in ambient and humidified conditions.

We studied how elevated air humidity can change the C budget of young silver birch stands in order to find out how climate change influences the C sequestration of northern deciduous forests. The study aims to determine the effect of elevated air humidity on the components of the C budget and on the C-sequestration capacity of a young birch forest. The main hypothesis is that increased air humidity affects the C sequestration of forest ecosystem. Working hypotheses of the study are: (1) C sequestration in plant (tree + understory) biomass is lower, and (2) C accumulation into soil is higher in conditions of increased air humidity.

2. Material and methods

2.1. Study site

The study was carried out in young silver birch (*Betula pendula* Roth) plots growing on the FAHM (Free Air Humidity Manipulation) experimental site, located in South-East Estonia (58°14′N, 27°18′E, altitude 40–48 m a.s.l.). The study area lies in the hemi-boreal forest zone in the transition zone between maritime and continental climates. The long-term average annual precipitation is 650 mm, the average temperature in July is 17.0 °C and −6.7 °C in January. The growing season with mean daily temperature above +5 °C lasts 175–180 days. The FAHM experiment has been established on 2.7 ha of former agricultural land; the soil is a fertile *Endogleyic Planosol* (WRB) with an average A-horizon thickness of 27 cm. Soil parameters did not differ between experimental plots before humidity manipulation was started. Soil characteristics in control and humidified plots for 0–10 cm soil layer in 2009 are published in Kukumägi et al. (2014).

The FAHM experiment contained three humidified and three control plots. Half of each experimental plot was planted with one-year-old silver birch (*Betula pendula* Roth) seedlings in the spring of 2006 and the other half with monoclonal hybrid aspens (*Populus tremula* L. × *P. tremuloides* Michx.), which we do not analyze in this study. The ground was plowed and levelled before planting. Inside the humidified plots, a computer-controlled system elevates relative air humidity by 7 percentage points during mist fumigation, on average, compared to the ambient, using misting technology and air blowers that homogenize humid air inside the plots; for a detailed technical description of the experimental facility see Kupper et al. (2011). Humidification treatment was applied every year from 2008 onwards during the growing season (May–September).

To investigate the impact of understory species composition and diversity on ecosystem functioning, two different types of herbaceous understory vegetation were established in every plot. The understory of half of each birch plot represents vegetation of post-clear cut forest, and the other half represents early-successional vegetation with low diversity and a strong dominance of a few grass species, such as that in abandoned arable fields. A detailed description of the sowing and planting of the two understory types: "forest" and "grasses" is published in Parts et al. (2013).

To estimate compartments of net primary production (NPP), an equal number of random samples were taken per plot and per understory type inside the plots, for both the control and humidification treatment.

2.2. Aboveground production

2.2.1. Trees

Productions of stem and branch biomass in 2009 were calculated as the differences between the respective biomasses in 2009 and 2008. Leaf production is considered to be equal to the leaf biomass. Birch aboveground biomass was estimated in August 2008 and in July–August 2009, when the process of aboveground biomass formation

Table 1
Regression equations for biomass of aboveground tree compartments (g) in 2008.

Regression equations		R^2
Stem biomass	$= 0.100 \times d^2h + 16.7$	0.98
Branch biomass	$= 0.0717 \times d^2h + 6.0$	0.98
Foliar biomass$_{Grasses}$	$= 0.0532 \times d^2h + 19.8$	0.98
Foliar biomass$_{Forest}$	$= 0.0542 \times d^2h + 7.8$	0.99

Abbreviations: d^2h – stem volume index (cm^3), and R^2 – coefficient of determination. $p < 0.001$ for all models. Grasses and Forest indicate two types of understories. Statistically insignificant intercepts are indicated in italics.

was largely completed. The aboveground biomasses for all trees in experimental plots in 2008 were calculated from the height and diameter of trees by using allometric regression equations (Table 1). The regression models in 2008 were developed on the basis of 12 randomly selected model trees (6 model trees per control and 6 per humidification treatment). The stems of the model trees were divided into four sections: the top shoot, the remaining stem of the living crown was divided into two equal layers, and the fourth section consisted of the lowest part of the stem, up to the beginning of the living crown. The crown sections were divided into stem (bark and wood were separated in subsamples), leaves, current-year shoots, and older branches compartments. The determination of dry masses of the compartments is described in Sellin et al. (2015). Tree height (h) and stem diameter at a 30-cm height (d$_s$) of all trees in experimental plots were measured yearly after the end of the vegetation period. Stem volume index (d$_s^2$h) was calculated and used as an independent variable in the regression models; the effect of humidification was not significant in any of the considered cases. The understory vegetation effect was significant for leaf biomass regression models (GLZ) in 2008; hence two separate models were used for the calculation of those biomasses.

Stem biomass in 2009 was calculated according a regression model ($R^2 = 0.96$) published in Sellin et al. (2015). Branch and leaf biomasses were calculated from stem biomass using biomass allocation data published in Sellin et al. (2015).

2.2.2. Understory

The aboveground biomass of the understory was estimated by harvesting twelve random samples (six samples per humidity manipulation treatment) from 0.5 m^2 area at the peak of aboveground biomass in 2009. Mosses were not sampled because their biomass was very small. In the laboratory, the fresh mass of understory samples was weighed and subsamples for estimating the dry mass were taken. Subsamples were dried to constant mass at 70 °C and weighed to 0.01 g. Net primary production of the aboveground part of the understory is considered to be equal to annually formed biomass, as the aboveground part of the understory is annual. Aboveground NPP of the understory was taken as the estimate for the respective annual litter flux.

2.3. Belowground production

2.3.1. Production of birch fine (d < 2 mm) roots and the belowground part of understory

Fine root and rhizome production was estimated for the A horizon (up to the sandy loam of the subsoil) by soil coring. Altogether 36 (18 per treatment) cylindrical soil cores (Ø 48–70 mm) were taken in July and September in 2009, and in May 2010. The soil cores were divided into three layers by depth: 0–10 cm, 10–20 cm, and 20 cm up to the subsoil. The roots and rhizomes were washed free of soil manually, and the following three compartments were separated under a microscope: (I) live roots and rhizomes of the understory; (II) live and (III) dead fine roots of birch. Belowground samples were dried at 70 °C for 48 h and weighed to 0.001 g. Understory fine-root and rhizome annual NPP was estimated by maximum-minimum method (Brunner et al., 2013), by subtracting the value of the lowest biomass (B$_{min}$), estimated

in May 2010, from the value of the highest biomass (B$_{max}$), estimated in July 2009 (formula (1)).

$$\text{Annual NPP} = B_{max} - B_{min} \tag{1}$$

For annual NPP of birch fine roots (formula (2)), we modified the formula (1) by adding the flux of dead roots (D).

$$\text{Annual NPP}_{birch} = (B_{max} - B_{min}) + (D_{max} - D_{min}) \tag{2}$$

The fine-root biomass of birch was the highest in September, and the belowground biomass of the understory in July 2009; the minimum biomasses were found in May 2010.

Birch fine-root biomass in 0–80 cm depth soil layer was obtained by using percentage of fine anchor roots in fine-root biomass of birch (10.2% in control and 8.1% in humidified plots), which was measured in FAHM experiment in 2011 (Rosenvald et al., 2014).

Birch fine-root turnover rate was calculated as annual root NPP divided by mean fine-root biomass (mean of maximum and minimum values). The turnover of the belowground part of the understory was calculated in the same way.

2.3.2. Biomass sequestration in birch root systems

To estimate coarse-root (d ≥ 2 mm) biomass of birches, 10 birch root systems (5 from control and 5 from humidification treatment) were excavated in 2007, and 10 soil blocks (1 × 1 square meter monoliths to a depth of 80 cm) around model birches were excavated in 2011. The excavated roots were carefully washed free of soil and separated into the coarse-root (d ≥ 2 mm diameter classes: 2 ≤ d < 5, 5 ≤ d < 10, 10 ≤ d < 20, d > 20 mm and stump) and fine-root (d < 2 mm) fractions in the laboratory. The coarse-root results obtained in 2007 and 2011 are comparable, since the planting density was one plant per 1 m^2 in both cases.

Birch coarse-root biomass in 2008 and 2009 was calculated according to an allometric regression model (formula (3)) obtained from the compiled data of both (2007 and 2011) years.

$$\text{Coarse root biomass (g m}^{-2}) = 0.0333 \times d_s^{2.52}, \tag{3}$$

where d$_s$ – stem diameter (mm) at a 30-cm height, $R^2 = 0.99$, $p < 0.001$.

The fast-developing fine-root system of young trees is not in a steady state; hence, additionally to coarse-root biomass, the biomass of fine roots also increases.

Fine-root biomass in 2008 was calculated according to regression models of fine-root dynamics (formulas (4), (5)) obtained from the 2007 and 2009 fine-root data, assuming that growth is exponential at that stage of stand development.

$$\text{In control plots, fine-root biomass (g m}^{-2}) = 0.0576e^{1.48A} \tag{4}$$

$$\text{In humidified plots, fine-root biomass (g m}^{-2}) = 0.0750e^{1.39A} \tag{5}$$

In the formulas, A – tree age (years).

Annual biomass sequestration in a birch root system (fine + coarse roots) was taken to be equal to the difference between the root system biomass in 2009 and 2008.

2.4. Tree litter

Altogether 12 litter traps (6 traps in control and 6 in humidified plots, each collecting from an area of 0.21 m^2) were installed under birches in 2008 and 2009. Litter collection started at the beginning of August and continued in ca. 2-week intervals until all leaves had abscised (by mid-November). Tree litter contained only leaf litter, because branch litter was negligible as trees were young. Litter samples were

dried at 70 °C to constant weight, and the dry mass of the samples was determined.

2.5. C in soil gas fluxes

2.5.1. Soil respiration

Soil respiration rates were measured monthly between 09.00 and 16.00 h during the growing season (May to October) in 2009 using a closed dynamic chamber method (PP Systems SRC-1 chamber with gas analyzer CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers) (Kukumägi et al., 2014). Six collars were inserted to a depth of 1–3 cm in the soil under silver birches in each experimental plot (altogether 18 collars in control and 18 in humidified plots). To measure only soil respiration, the green plants were cut if necessary. Control and humidified plots were measured in pairs in order to get representative data per day. Only total soil respiration was measured in 2009. To estimate the share of soil heterotrophic respiration, we used the ratio of heterotrophic respiration to total soil respiration estimated in a later experiment (unpublished data) in FAHM, which was carried out under similar weather conditions (rainy and cold summer) as those in 2009. Soil heterotrophic respiration was measured by the trenching method. Four geotextile (DuPont™ Plantex® Geoproma®) tubes (diameter 20 cm, length 35 cm) were inserted per experimental plot, and a collar for the soil respiration chamber was inserted inside each tube (altogether 12 collars in control and 12 in humidified plots). Trenching affected neither soil temperature nor moisture.

Soil temperature was measured simultaneously with respiration using an attached soil temperature probe STP-1 (PP Systems International Inc., USA) inserted at 5 cm depth. In addition, soil temperature (ST1 soil temperature probe; Delta-T Devices, Burwell, UK) was measured continuously in 3 replications at 15 cm depth in each experimental plot. There was a strong correlation (r > 0.99) between soil temperatures at 5 and 15 cm depths. Soil respiration depended exponentially on soil temperature (Kukumägi et al., 2014). The respiration flux for snow-free season (April–November) was calculated by the regression model Rs = a e^{bt}, where Rs is soil respiration and t is monthly mean soil temperature at 15 cm depth. Wintertime (December–March) soil CO_2 effluxes were estimated by adding 5% to the modeled snow-free season respiration fluxes (Varik et al., 2015).

2.5.2. Methane fluxes

Soil CH_4 fluxes were measured using the static chamber and gas-chromatography method (Hutchinson and Livingston, 1993). There were two replicate chambers in each of the six experimental plots (3 control and 3 humidified). The method of CH_4 measuring is described in detail in Hansen et al. (2013). Gas samples were collected once a month from July to December 2009. The annual CH_4 flux for the whole year of 2009 was calculated by using the average of the results measured in 2009. Methane flux had a seasonal pattern with a peak in summer. Measurements were taken in high, medium, and low flux periods. We assumed that each missing month represented one period and winter fluxes from January to March were negligible.

2.6. Soil leachate

Percolated water was collected by stainless steel plate lysimeters (each collecting from an area of 0.0627 m^2). The 12 lysimeters (two per birch plot) were installed in spring 2008 at a depth of 40 cm. The percolated water was collected every month when soil was unfrozen. Polyethylene tubes connected the lysimeters with water collectors (5000 ml polyethylene canisters installed at a depth of 1 m). Leached total C and total organic carbon (TOC) fluxes were calculated by multiplying the respective C content and water discharge.

2.7. Chemical analyses

Soil sampling and processing is described in Kukumägi et al. (2014). Total C content (C% per mass) of birch samples: stemwood (N = 9), stembark (N = 3), current year branches (N = 3), older branches (N = 3), fine (d < 2 mm) roots (N = 3), coarse roots (N = 4), leaf litter (N = 4), and the understory: aboveground (N = 6) and belowground (N = 4) per treatment were determined by the Vario TOC Solids Module; 950 °C (Elementar GmbH, Germany). Understory C% was estimated at maximum and minimum biomass, in July and May, respectively.

Total soil C% was determined by dry combustion method on a varioMAX CNS elemental analyzer (ELEMENTAR, Hessen, Germany). Total C and inorganic C of leachate were analyzed by Total Organic Carbon Analyzer TOC-V CPH/CPN (Shimadzu Corporation, Kyoto, Japan). TOC was calculated as the difference between total C and inorganic C. Soil organic matter content (SOM) was determined as loss on ignition at 360 °C. The N content (%) in plant subsamples was determined by standard Kjeldahl procedure using a Kjeltec Auto 1030 Analyzer (Foss Tecator AB, Höganäs, Sweden). The percentage of lignin in the dry mass of understory shoots was determined by the Fibertec™ M fiber analyzer (Foss Tecator AB, Höganäs, Sweden), according to the manufacturer's standard analytical procedures for acid detergent lignin. Total C% of plant material was analyzed in the Landscape Biogeochemistry Lab of the University of Tartu. All other analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

2.8. Compiling of the C budget

The C budgets in 2009 for humidified and control silver birch stands were compiled by using published and original results from the FAHM experiment. Annual biomass sequestration in aboveground compartments of the forest ecosystem occurred in stems and branches of trees, whereas birch leaf litter and shoots of the understory formed aboveground litter input into the soil. Belowground biomass sequestration occurred in tree root systems and in roots and rhizomes of the understory. Annual biomass sequestering into tree root system was calculated as the difference between root biomasses in July 2009 and July 2008. Biomass sequestering into the belowground part of the understory was taken as equal to the value measured in May 2010, before the beginning of the new vegetation period. Belowground litter input into the soil was estimated as the sum of the productions of tree fine roots and the belowground part of the understory. Root rhizodeposition and production of external mycelium were estimated roughly on the basis of available fine-root data and literature sources in the discussion and were not included in the C budget in Table 4.

Soil C losses were estimated as heterotrophic respiration and C leaching. Other fluxes: e.g. herbivory, photooxidation, BVOC emissions, lateral dissolved C transfer, and particulate C flow by erosion were assumed to be small and were not considered in the C budget.

To compile the C budget, NPP compartments were multiplied by respective C% divided to 100, and heterotrophic respiration as well as the flux of CH_4 were converted into C flux units. The net ecosystem production (NEP) was obtained by subtracting heterotrophic respiration and C leaching from the sum of NPP and methane oxidation. If the NEP > 0, the ecosystem acts as a C sink from the atmosphere, and if NEP < 0, the ecosystem is a C source.

2.9. Statistical analyses

The effect of humidification and understory type on plant and soil C% was assessed using analysis of variance (ANOVA); the assumptions were fulfilled in all cases. t-Test was used to detect difference in C% between aboveground and belowground part of understory. Generalized linear/nonlinear model (GLZ) analysis was used for detecting the influence of humidification and understory type on allometric regression models. The significant categorical factors and predictors were

determined using Type-3 LR tests. Statistical data analysis was carried out using Statistica, version 7.1 (StatSoft Inc., Tulsa, OK, USA) software package. The level of significance $\alpha = 0.05$ was accepted.

Uncertainty of carbon balance compartments was assessed according to Yanai et al. (2010) using the Monte Carlo approach. In particular, root mean square errors (RMSE) of the regression equations were used for perturbing the respective regression lines at each Monte Carlo iteration. In all other cases, standard errors were used for perturbation. Altogether 20,000 iterations were used for every budget component and the 95% interval was then produced by leaving out the 500 smallest and largest repetition results for each. The uncertainty of the C fluxes related to methane binding and leaching loss was not estimated, as the fluxes were negligible. For estimating NEP uncertainties, 200,000 repetitions were carried out. All uncertainty calculations were done using R (R Core Team, 2017).

3. Results

Elevated air humidity decreased birch biomass production (Table 2); the aboveground biomass production decreased 18% and root biomass production 9%. Birch fine-root turnover rate was similar in control and in humidified plots (1.04 and 0.94 year^{-1}, respectively), while the understory root turnover was 1.5 times faster under humidification (turnover rate 1.29 vs 0.88).

Humidification did not affect the C% of birch fractions, except those of older branches (Table 3). C% for understory were lower than for silver birch; C% in belowground part of the understory was lower than in the aboveground part irrespectively of treatment. Humidification decreased the C% of the belowground part of the understory at maximum biomass.

Soil C% (Table 3) and soil bulk density (1.36 g cm^{-3}) did not differ between humidified and control plots. Soil C stock in 0–10 cm soil layer in 2009 was 2026 and 1890 g C m^{-2} in control and humidified plots, respectively. The rapid decrease (~10%) of SOM was observed in both treatments from 2007 to 2008 as the result of ground preparation for planting. During the four years since humidification began (2008–2011), SOM in 0–10 cm soil layer decreased 15% in control plots and 9% in humidified plots from the values measured in 2007 (4.27 ± 0.19 and 3.82 ± 0.23 kg m^{-2}, respectively).

Humidified birch stands sequestered 4 t ha^{-1} year^{-1} C from the atmosphere, but control stands can be considered as C neutral (Table 4). The annual C input into plants was similar in control and humidified plots (483 vs 453 g C m^{-2}). However, the share of trees was lower and the share of understory was higher in NPP under humidification compared to ambient conditions. Humidification most strongly affected the production of understory roots and rhizomes, which was 2.6 times higher in humidified than that in control plots. Annual C input via litter into the soil amounted to 466 in control, and 703 g C m^{-2} year^{-1} in humidified plots. The annual C sequestration into plants and C input into the soil were almost equal in control plots; but in humidified plots, C input into the soil exceeded the accumulation in plants

by 250 g C m^{-2} year^{-1}. Methane was bound from the atmosphere into soil, but the respective C fluxes were negligible (0.058 and 0.028 g C m^{-2} year^{-1} in control and humidified plots, respectively).

Annual soil respiration was 1213 g C m^{-2} for control and 985 g C m^{-2} for humidified plots; annual heterotrophic respiration was 934 and 749 g C m^{-2}, respectively. Soil heterotrophic respiration exceeded C input by litter twofold in control plots (Table 4). In humidified plots, soil C losses were nearly covered (94%) by litter input.

The amount of percolated water was 128 ± 25 and 151 ± 47 mm in control and humidified plots respectively; the total C flux in leachate was 2.4 ± 0.6 and 3.5 ± 0.1 g C m^{-2} year^{-1} in control and humidified plots, respectively. DOC flux was 1.9 ± 0.5 in control and 2.6 ± 0.9 g C m^{-2} year^{-1} in humidified plots. C fluxes of leachate water did not differ between treatments.

The effect of humidification on N% of the understory and birch leaf litter was insignificant in 2009. However, for the belowground part of the understory, there was a tendency for lower N% in humidified plots (1.36 ± 0.12) compared to control plots (1.60 ± 0.09). The lignin % in aboveground understory was low (7.63 ± 0.73 in control plots and 6.64 ± 0.32% in humidified plots) and was not impacted by humidification.

Uncertainty limits in the estimation of compartments of C balance for control and humidified ecosystems were considerable (Table 5). The majority of the uncertainty intervals were shifted towards smaller

Table 3
The mean (±SE) C content (%) of tree fractions and litter, understory, and soil in control and humidified silver birch plots.

		C %	
		Control	Humid.
Birch fractions	Stem bark	53.2 ± 1.3	54.7 ± 0.2
	Stem wood	51.2 ± 0.5	51.1 ± 0.4
	Older branches	**53.0 ± 0.5**	**55.3 ± 0.7**
	Current year shoots	53.2 ± 0.7	53.7 ± 0.4
	Fine roots <2 mm	46.8 ± 1.0	47.8 ± 0.25
	Coarse roots	50.8 ± 0.3	50.3 ± 0.5
	Leaf litter	53.8 ± 0.3	53.8 ± 0.3
Understory aboveground		42.3 ± 0.6	41.4 ± 0.5
Understory belowground	At max. biomass	**38.7 ± 0.6**	**35.6 ± 1.0**
	At min. biomass	42.3 ± 0.8	41.9 ± 0.7
Soil (0–10 cm)		1.49 ± 0.12	1.39 ± 0.06

Abbreviation: Humid. – humidified plots. Differences between treatments ($p < 0.05$, t-test) are indicated in bold.

Table 2
Tree biomass and production in control and humidified silver birch plots.

	Biomass (g m^{-2})				Production (g m^{-2} year^{-1})	
	2008		2009		2009	
	Control	Hum	Control	Hum	Control	Hum
Aboveground					680	561
Stem	160	152	518[a]	437[a]	358	285
Branches	109	102	234	225	125	123
Leaves	90	86	197	153	197	153
Belowground					330	300
Coarse roots	96	98	272	253	176	155
Fine roots (0–80 cm)	23	25	103	84	154	145

Abbreviation: Hum – humidified plots.
[a] Stem biomasses in 2009 are published in Sellin et al. (2015).

Table 4
C budgets of birch stands in control and humidified plots.

		C (g m^{-2} year^{-1})	
		Control	Humid.
INPUT FLUXES	**INPUT**	949	1156
	Sequestered in plants (1)	483	453
	Aboveground (stem + branches)	251	215
Trees	Root system	122	105
Understory	Aboveground	0	0
	Belowground	110	133
	Litter input into soil (2)	466	703
	Aboveground litterfall (sum)	223	186
	Tree leaf litter	85	66
	Understory	138	120
	Belowground litter (sum)	244	517
	Tree fine roots	72	69
Soil	Understory	172	448
	CH$_4$ oxidation (3)	<0.1	<0.1
OUTPUT FLUXES	**OUTPUT**	936	752
Soil	**Soil heterotrophic respiration (4)**	934	749
	C leaching (5)	2.4	3.5
CHANGE (NEP)	**INPUT − OUTPUT (1) + (2) + (3) − (4) − (5)**	13	404

Abbreviation: Humid. – humidified plots.

Table 5
Uncertainty in estimation of compartments of C balance. The 95% uncertainty intervals were calculated from regression equations (indicated by *) and other estimates using Monte Carlo simulation with 20,000 iterations.

	Uncertainty intervals (g C m^{-2} year^{-1})			
	Control		Humid.	
	Lower limit	Upper limit	Lower limit	Upper limit
Trees aboveground (stem + branches)*	206	307	156	273
Trees root system*	68	196	58	177
Understory aboveground	0	0	0	0
Understory belowground	79	140	80	185
Tree leaf litter	69	101	42	90
Understory aboveground litter	99	177	100	140
Tree fine root litter	28	116	20	117
Understory belowground litter	103	241	338	559
Soil heterotrophic respiration*	726	1346	556	1210
CHANGE	−411	258	−83	647

Abbreviation: Humid. – humidified plots.

values for humidification than for the control treatment. The uncertainty intervals for belowground litter of understory in control and humidification treatments did not overlap, showing the biggest difference between treatments.

4. Discussion

Our results show that climate change towards higher air humidity, predicted for higher latitudes can significantly affect C cycling and sequestration in the young deciduous forests. Two years of elevated air humidity treatment increased remarkably the C input into the soil of a young birch forest ecosystem. The main reason for such an increase was the higher root litter input into the soil, brought about by the more than two-fold increase in belowground biomass production of the understory under humidification (Kukumägi et al., 2014). The increased root biomass (root:shoot ratio) is a common stress reaction of herbs in case of unfavourable water and nutrient conditions (Reich, 2002). Our results show that, similarly to other stress factors, also elevated air humidity causes an essential increase in the root:shoot ratio of herbs. The analogous stress response of birch roots appeared later – after four years of humidification, when the biomass allocation into fine roots of birches was also increased in humidified plots (Rosenvald et al., 2014).

The first hypothesis remained unproven, as total C sequestration in plants was similar in humidified and ambient conditions. However, the effect of humidification on C cycle was significant, because humidification increased C sequestration in the understory but decreased it in trees. Despite of remarkably increased production of roots and rhizomes of understory in humidified plots, the aboveground biomass of the understory (Kukumägi et al., 2014) and also its N%, essential for photosynthesis, did not differ between humidified and control plots. Hence N use efficiency of understory shoots should be higher under elevated air humidity in order to gain two times higher belowground production.

Smaller biomass production of birches under humidified conditions can be partly explained by the decreased photosynthetic capacity of leaves (Sellin et al., 2013). However, also higher tree root competition with understory roots, and temporary excess of soil moisture with a concomitant decrease in soil oxygen content are likely responsible for impeding tree growth in humidified plots (Sellin et al., 2017). In terms of above-ground growth, the competitive performance of humidified birches in 2009 was significantly weaker compared to trees with similar social status in control stands (Tullus et al., 2017). It seems that understory plants have competitive advantages in comparison to trees under humidification. This is reflected in the abovementioned different effects on biomass productions, but also on N% – birch leaves contained less N in humidified plots (Sellin et al., 2013), but N% of understory shoots was not affected by humidification (Kukumägi et al., 2014). Additionally,

birch leaf area index, related to shading of understory by trees, was 17% lower in humidified plots (Sellin et al., 2015), resulting in better light availability for understory compared to that in control plots.

Processes taking place in the soil are most important in calculations of forest C budget, because on average about 25–35% of the forest C is contained in vegetation and 65–75% in the soil (Malhi et al., 2015), and soil respiration typically comprises 80% of the total gross primary production (Janssens et al., 2001). Our second hypothesis, that C accumulation into soil increases under elevated air humidity, appeared to be true. In humidified plots, soil C input (litter) was only slightly exceeded by the C loss (heterotrophic respiration), but in control plots, soil C input was two times smaller than C loss. Hence, part of the heterotrophic respiration probably occurred at the expense of formerly accumulated soil C (not of recent litter input). However, there were no significant changes in soil C% from 2007 to 2011 in control and humidified plots (unpublished data), most probably due to the short time interval. Nevertheless, four years of humidification decreased SOM less in humidified plots than in control plots (9 vs 15% from initial value).

The substrate quality for decomposers differed between treatments, and affected significantly bacterial communities in FAHM experiment (Truu et al., 2017). Humidification did not affect the N% (Kukumägi et al., 2014) C% and lignin % of the aboveground part of the understory, but decreased N% (unpublished data) and C% of the belowground part of the understory. In addition to substrate amount and quality, soil heterotrophic respiration is affected also by environmental factors (soil temperature, moisture, pH). Soil temperature did not differ between treatments, but soil moisture content was higher in humidified plots. Kukumägi et al. (2014) found that the total soil respiration was negatively related to soil moisture content in the rainy summer of 2009 (precipitation data are published in Godbold et al., 2014); however, soil moisture impacted respiration weakly. It has been found that an increase of soil pH can enhance soil heterotrophic respiration (Rousk et al., 2009); however, in our study the effect of pH was not revealed, probably as the increase (<0.3 pH units) was small (Kukumägi et al., 2014; Parts et al., 2013). On the one hand, increased soil pH and substrate input for heterotrophic respiration favoured microbial activity, but on the other hand, more humid air decreased transpiration and brought about higher and possibly even excessive soil moisture content for decomposers. Hence, elevated air humidity affects heterotrophic respiration in different ways and via different processes.

The main C storage in hemiboreal silver birch stands growing on fertile soils was located in the soil during the first 30 years, and after that, in tree biomass (Uri et al., 2012). Correspondingly, in our young, 5-year-old experimental stands, C sequestration in tree biomass was smaller than the input to the soil. Our control stand sequestered less C than older (13–45 years old) birch stands reported in Varik et al. (2015), as trees were smaller (lower accumulation in tree biomass) and soil respiration was higher. Soil respiration of older birch stands varied between 618 and 972 g C m^{-2} year^{-1} (Varik et al., 2015), being smaller than the flux in our control stands (1213 g C m^{-2} year^{-1}), which is comparable rather to the fluxes measured in fertile grasslands on mineral soils in Europe (1166 and 1246 g C m^{-2} year^{-1}, Bahn et al., 2008). Usually, 0 to 10 years old temperate and boreal forests act as C sources to the atmosphere (Pregitzer and Euskirchen, 2004), whereas our ambient birch stands can be considered as C neutral. However, according to the C budget of humidified plots, birch forests can be C sinks already at the age of five years in more humid climate.

Among considerable C fluxes which were not included to the budget (root exudates, production of external hyphae, photooxidation, herbivory), the most essential flux of C is most probably root exudates. It was estimated to be from 90 to 104 g C m^{-2} year^{-1} for 8-year-old yellow birch stands (Phillips and Fahey, 2005). The production of ectomycorrhizal mycelia varies tremendously between forest sites (Ekblad et al., 2016) and among exploration types of EcM fungi (Wallander et al., 2013). In the FAHM experiment, less mycelium per ectomycorrhizal root tip (Parts et al., 2013), but higher average biomass

of absorptive EcM roots per m^2 was found under humidification (Rosenvald et al., 2014). Using proportional colonization frequencies of EcM fungi (Parts et al., 2013), mycelial biomass factors for different exploration types (Wallander et al., 2013; Weigt et al., 2012a,b), the average biomass of absorptive EcM roots (Rosenvald et al., 2014), and the average lifespan of hyphae – 9 days (Godbold et al., 2006) for control and humidified plots, the roughly estimated flux to EcM mycelial biomass production might amount to 39 kg m^{-2} and 66 kg m^{-2} year^{-1}, respectively. Hence the respective C fluxes should be at least two times smaller. C loss by photooxidation was assumed to be small in 2009 due to the rainy summer. We did not have enough data to estimate the NPP of the external mycelium of arbuscular fungi. No massive damage of herbivores was detected in the study year. Hence, the fluxes excluded from our calculations are assumed to be too small to impact appreciably our C budgets.

Interpreting the results as indicators of the consequences of climate change, it must be considered that we studied only the preliminary effect of humidification on C budget and discarded the fact that, in climate scenarios, higher humidity in high latitudes is associated also with increased air temperature and longer vegetation period. We have some evidence that the influence of humidification may partly decrease in the longer term, e.g. aboveground biomass production of birches recovered after four years of treatment (Rosenvald et al., 2014), and understory biomass considerably decreased when birch canopy closed and did not differ between treatments (Torga et al., 2017). Hence the long-term effect of humidification on the carbon sequestration of a deciduous forest ecosystem is significant, but remains presumably smaller than the response found in young forest.

5. Conclusions

Elevated atmospheric humidity shaped the C cycle of young silver birch stands. The first hypothesis of this work remained unproven. Elevated air humidity did not decrease annual C sequestration in plant biomass, as the decrease in tree production was compensated by the C sequestration in the belowground part of the understory. The second hypothesis was true – C accumulation into soil was higher in humidified conditions. Elevated humidity enhanced ecosystem C sequestration mainly due to a two-fold increase in understory root and rhizomes production, resulting in a bigger litter input into the soil. Most of C loss via heterotrophic respiration was counterbalanced by litter input in humidified stands, but not in control plots, where heterotrophic respiration exceeded twice the litter input. Due to a short time interval, significant changes in soil C pools were not found. In summary, young birch stands growing in ambient conditions can be considered as C neutral, but humidified stands sequestered C and thus mitigated the increase in CO_2 concentration in the atmosphere.

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